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Decline of the Chiricahua Leopard Frog in Arizona Mediated by Introduced Species

DECLINE OF THE CHIRICAHUA LEOPARD FROG IN ARIZONA

MEDIATED BY INTRODUCED SPECIES

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ABSTRACT

Introduced species are a worldwide problem and a major constituent of the global biodiversity crisis. In the American West, this crisis is severe for 13 of the 15 native species of "true frogs" of the family Ranidae. Not counting the two species with eastern distributions, all extant species are declining in most subregions of this large area. Introduced species have been implicated in at least some of the frog declines in each subregion. Nevertheless, other causes of decline, most only locally or weakly documented, are more widely recognized. Widespread declines of leopard frogs (Rana pipiens complex) in Arizona represent a relatively newly identified case of amphibian decline. We present evidence that the Chiricahua leopard frog does not co-occur with non-indigenous species in southeastern Arizona, which are now widespread and diverse in all landscapes. Historical data and observations at specific localities show that leopard frogs have been replaced by introduced species. Bullfrogs and centrarchid fishes are shown statistically to have significantly displaced populations of this leopard frog; catfishes and trout are suspected of doing so as well. Introduced species occur in dense populations, particularly in modified habitats and in the absence of many predators from their native ranges. The stable pond and pool habitat of the Chiricahua leopard frog places it in direct and lethal contact with alien species. In contrast, an isolated population of the Plains leopard frog in southern Arizona persists with introduced species in highly varying wetland environments that it appears to tolerate better than the non-natives. We report successful re-introduction of Chiricahua leopard frogs in an enclosure excluding the exotics, and suggest that existing ranch stock ponds may provide ideal refugia for this and some other species during the current crisis mediated primarily by introduced species.

INTRODUCTION

There is increasing, but still insufficient, awareness that introduced species are a major, worldwide part of the biodiversity crisis. Biogeographically isolated areas such as Australia have had well known debacles (Lever, 1994) involving such mundane taxa as European rabbits (Oryctolagus cuniculus) and giant toads (Bufo marinus). True islands have been especially hard hit. In Guam, the introduced brown tree snake (Boiga irregularis) is eliminating a host of native bird and lizard species (see Savidge, 1987; Fritts and Rodda, 1995; Rodda and Fritts 1992). In the West Indies, endemic iguanas and unique solenodont mammals are at or approaching extinction in the face of habitat destruction and introduced cats, dogs, and mongooses (Burghardt and Rand 1982; Thornback and Jenkins 1982; Nowak 1991). Island-nesting seabirds may also be highly vulnerable (Hatch and Piatt, 1995). These problems may be caused primarily by unsaturated communities in biogeographically isolated areas, and by the resulting naiveté of native insular species in the face of new and intense competitors, and more especially, highly evolved predators.

Major crises caused primarily by introduced species in freshwaters, especially lakes, are now increasingly documented for major biogeographic areas including in Africa (Witte et al. 1992; Ogutu-Ohwayo 1993; Bruton and van As, 1986), central America and Mexico (Zaret and Paine, 1973; Contreras and Escalante, 1984), and North America (Miller, 1961; Moyle, 1986; Moyle et al., 1986; Minckley and Deacon, 1991; Edsall et al., 1995; Hansen and Peck, 1995), and introduced fishes are also known to have caused problems on other continents (McKay, 1984; McDowall, 1984; Lelak, 1987). Miller et al., (1989) provided the best quantitative summary of causes of extinction, based on the North American fish fauna; they estimated that introduced species were involved in 68% of the extinctions, compared to 73% involvement of habitat changes (destruction, degradation, modification), with other factors as 38% involvement or lower. Despite this, fisheries biologists often treat exotic species introduction as a lesser,

or last-listed cause for decline (e.g., Moyle and Leidy, 1992; Warren and Burr, 1994), there continues to be disagreement at the professional level about the appropriateness of exotic species introductions (Horak, 1994, and Moyle and Li, 1994; responses to Lassuy, 1994), and the American Fisheries Society (1994) "visionary" programmatic statement only mentions exotic species twice, almost in passing.

A failure to recognize or countenance the full severity of the introduced species problem is both unjustified and consequential. The problem is not confined to fishes, animals on islands, or even to animals. Exotic plants are beginning to seriously damage native ecosystems, often becoming severely noxious after decades of acclimation or evolution following initial introduction (Baker, 1986; Kruger et al., 1986). For indigenous faunas, currently documented effects of species introductions are for especially severe cases, where non-indigenous keystone species--often, but not always, predators--go rampaging through entire species groups or food webs. Indirect effects, less potent interactions, and evolutionary adjustments will have further effects that will extend through trophic cascades; and the effects of already-introduced plants and animals may well qualitatively exceed the effects we can now demonstrate or even understand. Furthermore, whereas pollution and even habitat damage can potentially be remediated and repaired, established exotic species may be impossible to dislodge (Clout, 1995), given current technology and knowledge of ecological community dynamics.

Species introductions are often made to satisfy relatively non-essential desires, such as enhancement of sport-fishing; or they may be short-sighted, as when mosquitofish are used for mosquito control instead of indigenous species that are equal to the task but less well known (e.g., Walters and Legner, 1980). Despite these facts, laws are relatively weak or nonexistent, governmental agencies worldwide are often still attempting ecosystem management using species introductions into the wild, and it remains incredibly easy for individuals to translocate organisms. Further, the public is not fully aware of the problem they pose, and it may even seem inconvenient to confront such a difficult sociological problem. Conservation efforts rely in substantial part on support from hunting and fishing enthusiasts, as well as on the growing conservation and nature oriented public sector. Widespread agreement among all these major groups is crucial to forestall the spread of exotics by uninformed or disgruntled individuals or groups. Therefore, it is essential (1) to clearly and consistently recognize and publicize the problem in all its facets, and (2) to continue to generate examples and enhance our understanding of the processes leading to effects of introduced species on ecosystems and specific species.

It now appears that essentially all of the native ranid frogs (genus Rana) of western North America are in decline (Vial and Saylor, 1993, and therein; Jennings, 1995; Sredl and Howland, 1995) or have disappeared (Hale, et al., 1995; Stebbins, 1985), and these declines have been reported from every region (Arizona--Clarkson and Rorabaugh, 1989; California--Jennings, 1995; Colorado--Hammerson, 1982; Corn and Fogelman, 1984; Pacific Northwest--Leonard et al., 1993; Bahls, 1992 and therein). This may also be part of a global decline of amphibians (e.g., Phillips, 1990) that apparently has multiple causes.

Introduced predators and competitors have been directly associated with ranid frog declines in all regions of western North America (Bahls, 1992; Bradford, 1989; Bradford et al., 1993; Clarkson and Rorabaugh, 1989; Dumas, 1966; Fellers and Drost, 1993; Hammerson, 1982; Hayes and Jennings, 1986, 1988; Leonard et al., 1993; Liss and Larson, 1991; McAllister et al., 1993; Moyle, 1973; Rosen and Schwalbe, 1995; Rosen et al., 1995; Schwalbe and Rosen, 1988; Vitt and Ohmart, 1978), and this problem is undoubtedly affecting other amphibians in the American West (e.g., Collins et al., 1988) and elsewhere in the world (e.g., Brönmark and Edenhamn, 1994). There is also evidence that North American amphibians may be impacted by ultra-violet radiation (Blaustein et al., 1994), acid rain (Harte and

Hoffman, 1989), and heavy metal toxicity (Hale, et al., 1995), although in western North America none of these effects is as apparently ubiquitous as introduced species.

Already-substantial and accumulating evidence for effects of introduced species has been and is being obtained by natural historians who would be unlikely to "experimentally" introduce harmful exotics in the name of demonstrating the apparently obvious. Meanwhile, problems associated with ozone depletion and acid rain have captured the public and scientific eye, seeming to be modern problems which are being studied by sophisticated methods, are possibly relevant to human health and ecology, and may be resolved with a technological (rather than sociological) fix. Natural historians are inherently disadvantaged by a scientific culture demanding field experimentation or mathematical modelling as a pre-requisite for intellectual acceptance. The observations natural historians make are often correlative, or may seem unsubstantiated by ecological theory, and they are therefore often publicized in relatively unknown journals or remain in the gray literature. Nonetheless the volume and consistency of these observations is becoming impressive.

In this study, we present correlative data indicating a potent effect of non-indigenous species on the formerly abundant and widespread ranid, the Chiricahua leopard frog, in southern Arizona, which is now known to have suffered dramatic population decline (Clarkson and Rorabaugh, 1989; Sredl and Howland, 1995; R. Jennings, C. Painter, personal communications) throughout its range in the U.S. (Arizona and New Mexico). In this report, we treat the problems related to introduced vertebrates, which are widespread in the study area, but we ignore the effects of introduced crayfishes, which are not yet ubiquitous in our area. We supplement this finding by adding historical perspective and niche analysis at key study sites. Finally, we describe early success with a re-establishment effort guided by the hypothesis that introduced species are primarily responsible for decline of the Chiricahua leopard frog.

STUDY AREA AND SPECIES

We conducted this study in the desert grassland region of southeastern Arizona in Pima, Santa Cruz, Graham, and Cochise counties. This area, bounded on the west by the Baboquivari Mountains, on the north by the Rincon and Pinaleño mountains, and on the east by the Peloncillo Mountains, encompasses the original range of the Chiricahua leopard frog in southern Arizona. At lower elevations, Sonoran and Chihuahuan desertscrub grade into desert grassland at about 1000 m elevation. Desert grassland gives way to oak woodland at around 1600 m, although in some areas well-developed Chihuahuan desertscrub occurs between extensive grass-dominated valley floors and oak and pine-dominated mountain slopes.

Small permanent streams and permanent-water ciénegas (often much reduced) occur on each valley floor in the region except the Sulphur Springs and San Simon (Hendrickson and Minckley, 1985). A limited number of small perennial streams also occur in oak-pine habitats in the Chiricahua, Huachuca, Santa Rita, and Pajarito mountains; other mountain ranges in the area have tiny springs and semi-perennial streams, and lack native fish (Minckley, 1973). Stock ponds created and used for cattle ranching occur throughout the area. They are usually less than 0.5 ha in size, have varied maximum depths from ca. 1-3.5 m, and vary from runoff fed and ephemeral to perennial with essentially invariant water levels maintained by groundwater. In agricultural areas of the Sulphur Springs Valley, some ponds are used to store and deliver irrigation water, and rise and fall frequently and over a short time.

At least as recently as the early 1950's, the floor of the Sulphur Springs Valley was inundated

over large areas during the summer monsoonal rains (C.H. Lowe, personal communication), and this remains true in limited areas of Whitewater Draw. The Willcox Playa in the northern Sulphur Springs Valley may be too saline for frogs when it floods, but a large electrical power plant there maintains the largest perennial wetland in southern Arizona (over 1 km^2) for ash-disposal. Some lowland streams and ciénegas have been degraded or destroyed, especially the San Simon Ciénega and River, during the past 100 yr (Hendrickson and Minckley, 1985). However, the area has always had little natural surface water, and the Sulphur Springs Valley was probably largely lacking in perennial surface water under natural conditions.

The Chiricahua leopard frog (Rana chiricahuensis) is a large (frequently exceeding 100 mm snout-vent length [SVL]) ranid frog inhabiting primarily perennial streams, springs, and marshes (Frost and Bagnara, 1977), as well as stock ponds (Scott and Jennings, 1985), in southeastern Arizona and southwestern New Mexico (Jennings and Scott, 1993), and along the Mogollon Rim and White Mountains in both states. In Mexico, it extends through eastern Sonora and central western Chihuahua south into central Durango (Platz and Mecham, 1979; Stebbins, 1985). Within stream or spring systems, this leopard frog is frequently associated closely with deep pools or ponds (personal observations in Arizona). It formerly existed in all major valley springs and streams in the desert grassland and woodland of southeastern Arizona, including San Bernardino National Wildlife Refuge (SBNWR), Whitewater Draw, San Pedro River, Santa Cruz River, Cienega Creek, Arivaca Creek, and Altar Valley (Clarkson and Rorabaugh, 1989 and therein; personal observations), often in great numbers (Wright and Wright, 1949; Frost and Bagnara, 1977), and it has suffered drastic declines in the past two decades (Clarkson and Rorabaugh, 1989; M. Sredl, R. Jennings, J. Bagnara, J. Platz, personal communications).

The lowland leopard frog (R. yavapaiensis) enters the extreme northwest and southeast margins of the study region (Stebbins, 1985; M. Sredl, personal communication; personal observations), and may be extirpated from the western range area, in southeastern Pima County. It is usually, but not always, smaller in maximum adult size than the Chiricahua leopard frog. These two species may occur in similar habitat (Frost and Platz, 1983; Scott and Jennings, 1985), although our observations in southern Arizona show the lowland form to be primarily in desert or low desert grassland; it is most abundant in shallow, flowing streams with few pools and with moderate or little bank vegetation; in contrast, the Chiricahua leopard frog is usually found in more stable and deeper aquatic habitat. The shallow stream habitats have few introduced animals; and the lowland leopard frog still occurs widely and in numbers in central Arizona (Clarkson and Rorabaugh, 1989; M. Sredl, personal communication).

The plains leopard frog (R. blairi) exists as an isolated population in the grasslands of the Sulphur Springs Valley in southeastern Arizona, approximately 300 km from the nearest population in New Mexico (Stebbins, 1985). This species is typically found in semi-permanent pools, ponds, and playas (Frost and Bagnara, 1977; Scott and Jennings, 1985), especially those in the Sulphur Springs Valley that have dramatic fluctuations in surface area (personal observations). In southeastern Arizona, it has a spring-summer breeding pattern, in contrast to the fall-early spring breeding of the lowland leopard frog and the late winter-late summer breeding of the Chiricahua leopard frog (Collins and Lewis, 1979; Frost and Platz, 1983; Platz, 1993; and personal observations).

In addition to the native leopard frogs, perennial waters we surveyed yielded non-indigenous species including bullfrogs (R. catesbeiana), tiger salamanders (Ambystoma tigrinum), and 11 species of fishes. Perennial waters we surveyed also revealed 7 native fishes. Six other species of native frogs, usually found in ephemeral waters, were occasionally recorded from perennial waters; and we recorded

two turtle species and three garter snake species at study localities. Details can be found in Rosen et al. (1995).

METHODS

We surveyed intensively for leopard frogs in southeastern Arizona primarily during the drought summer of 1994. We attempted an exhaustive survey of perennial waters in the Chiricahua Mountain region during summer 1994 (Rosen and Schwalbe, 1995), as well as in the Buenos Aires National Wildlife Refuge region in the Altar Valley. We additionally surveyed intensively in the San Luis, Atascosa-Tumacacori-Pajarito Mountain complex, and visited numerous perennial and semi-perennial water sites in the Santa Rita and Santa Catalina mountains, Avra Valley, and in Cienega Creek: in these regions, we focused at and near historically known leopard frog localities.

We visited all known localities for the Chiricahua leopard frog and the plains leopard frog in the Chiricahua Mountains and surrounding Sulphur Springs, San Bernardino, and San Simon valleys, and in the Dragoon and Peloncillo mountains, Cochise and Graham counties, as determined from Clarkson and Rorabaugh (1989, and therein), surveys of museum collection localities, and interviews with herpetologists familiar with the area. We also sampled other accessible perennial or semi-perennial waters, attempting to visit all potential leopard frog habitat areas; occasionally, site access was denied by private landowners. Whenever possible, we discussed water permanence and faunal observations with landholders, significantly enhancing our ability to locate good sites for frogs.

Most of the work reported here was done May-August 1994, a time of drought in southeast Arizona; eleven of the sites were visited only in 1992 or 1993. The 1994 work was prior to a tardy onset of monsoonal rains, some areas receiving no runoff until at least September--over 2 months late. It was a dry summer following a dry winter in a longer term drought beginning in the mid-1980's. Whereas the aquatic fauna suffered during this drought, we capitalized on the opportunity to determine with some certainty the permanence for each water source. When we arrived at or near what we estimated to be the drought minimum water level, we recorded the deepest point of each site by wading or diving. These estimates represent 10-20 yr depth minima, based on interviews with resident landholders and land managers. Finally, we revisited a number of sites that were dry in early summer but subsequently filled with runoff, sampling as described above.

At each site, we approached the wetland habitat slowly, using binoculars for visual observation of frogs or surfacing salamanders and turtles, as well as for fishes. We then walked along the water margin counting frogs or other animals as they moved or were otherwise observed. Finally, we sampled each site with dipnets (6-mm-mesh) and seines (3- x 1-m and 8- x 1.8-m; 6-mm- mesh) to confirm species identifications and determine relative abundances for tadpoles, salamanders, turtles, and fishes. We also made nocturnal visits to sites with leopard frogs, and other sites when diurnal surveys were insufficient.

The extreme drought in 1994 allowed us to focus our survey exclusively on fully perennial waters. These drought refugia are highly significant for the arid lands biota. In wetter years, interpretation of negative results for any species or site would be complicated by the possibility that the site had been dry and had not yet been re-colonized by or re-stocked with aquatic animals. Based on our interviews, perennial waters in 1994 had essentially all been perennial since 1989, and most had been perennial since about 1976. Possibly none of them had thoroughly dried since 1976. We were thus able to report on samples from a time when faunal patterns were most clear, and when critical drought refugia for leopard

frogs were most readily identifiable.

RESULTS AND DISCUSSION

I. Chiricahua Leopard Frog.

Survey Results. We investigated a total of 175 wetland sites, of which 107 had surface water during our visits. A few perennial waters surveyed in 1994 contained no perennial-water vertebrates. These bedrock plunge-pool habitats will be discussed further below. All other perennial waters we surveyed during 1993-1994 contained either introduced fishes (n=34 localities), introduced tiger salamanders Ambystoma tigrinum mavortium (n=13 localities), and/or bullfrogs (n=31 localities), or they contained native Chiricahua leopard frogs (n=19 localities). Chiricahua leopard frogs were with centrarchid fish (green sunfish, Lepomis cyanellus) in one case of limited overlap, and with tiger salamanders twice (Table 1).

The single co-occurrence of Chiricahua leopard frogs and alien fish (green sunfish) was seen at low water in late July 1994, in central Peck Canyon, Atascosa Mountains, Santa Cruz County. Three large adult frogs were found in a 0.5 km perennial reach with many green sunfish 7-20 cm total length. There were no tadpoles or juvenile frogs. One case of co-occurrence of Chiricahua leopard frogs and tiger salamanders may present a similar situation. In Tom Ketchum Tank, Pedrogosa Mountains, Cochise County, two adult frogs were found with a small number of very large (ca. 30 cm total length) paedomorphic cannibal morph (Collins, 1981) salamanders: again, frog population density was low, and breeding was not in evidence. In both cases, the observed frogs appear to be derived from healthy or formerly healthy populations 2-7 km distant.

In the second instance of tiger salamander-Chiricahua leopard frog co-occurrence, the only known 1994 population of Chiricahua leopard frogs in Avra-Altar Valley, at Garcia Tank, Pima County, consisted of about 75-120 observable juveniles in a pond with a small number of large branchiate tiger salamanders. Whether this situation is stable or at least tenable for the frogs is unclear (see Sredl and Collins, 1991), but three nearby ponds with higher salamander densities had no frogs in 1994. None of the frogs survived into spring 1995, but tadpoles in two large size classes did, along with a large crop of small tiger salamander larvae. We are continuing to monitor this site.

Habitat Characteristics and Historical Perspective. The Chiricahua leopard frog was not found during 1992-1994 in the natural, perennial water habitats on the valley floors of southeastern Arizona (Sredl and Howland, 1995; personal observations), where it formerly abounded. In each of our surveys, these sites were occupied by large populations of either bullfrogs or centrarchid fishes, or both. All valley floor wetlands are highly modified, primarily by the addition of small and large check dams and levees that create lentic waters varying from deep pools to large ponds. Dams restrict the effectiveness of flooding for reduction or elimination of exotic fishes (see Minckley and Meffe, 1987), and they probably also are habitats where eastern U.S. species are at maximum competitive and predatory advantage. We observed non-indigenous species particularly in these habitat types during our surveys of natural wetland areas.

Similarly, in 1994 the Chiricahua leopard frog was absent from all major montane stream systems in southern Arizona with two exceptions--at Sycamore Canyon in the Pajarito Mountains, and Leslie Canyon National Wildlife Refuge in the Swisshelm Mountains--although they formerly occurred in all of

them. All of these sites from which the Chiricahua leopard frog disappeared have modified habitat in the form of dams that create ponds or small lakes, and these artificial lentic habitats contain a diversity and abundance of alien species, primarily predatory fishes. Museum records demonstrate that Chiricahua leopard frogs formerly occurred in these modified habitats, and Rosen et al. (1995) showed that the time scale of fish introductions in the region is consistent with the recent population collapse of the Chiricahua leopard frog. Sycamore Canyon and Leslie Canyon lacked both substantial habitat modification and non-indigenous species, suggesting that habitat modification may be a key, or at least important, antecedent to introduced species effects in this region. Clearly documenting and demonstrating such a synergism, and attempting to reverse it, are perhaps the greatest challenges in conservation in this and perhaps several other regions of the American West (see Moyle, 1973; Hayes and Jennings, 1986, 1988; Jennings and Hayes, 1994).

In stock tanks and small mountain streams and springs, the Chiricahua leopard frog was present in shallow-water habitats, many of which nearly dried in 1994 (Rosen et al., 1995), whereas introduced species were present in deeper and more highly oxygenated sites. In one case, S. Hale conducted a thorough survey of Peck Canyon and all of its side canyons in 1990, and we did a repeat survey in 1994. The 1994 situation was similar to that observed in 1990, except that the only thriving population of Chiricahua leopard frogs in 1990, in the Fresnal Canyon side drainage (S. Hale, personal communication), had been totally replaced in 1994 by a newly present, large population of introduced green sunfish (Lepomis cyanellus). We were able to document other cases of apparent elimination of this leopard frog by introduced species based on museum locality records, although the time of replacement could not be so accurately specified (Table 2).

The absence of the Chiricahua leopard frog from the major natural wetland habitats in southern Arizona is both significant and disturbing. First, we and other experienced field herpetologists (especially M. Sredl, E. Wallace, J. Rorabaugh, R. Zweifel, W. Sherbrooke, J. Platz, S. Hale, P. Holm, personal communications) have searched intensively and repeatedly at these sites, and the absence of the frogs is likely to be real. Second, the absence has a powerful implication from the standpoint of metapopulation dynamics on the landscape. The ongoing restriction of Chiricahua leopard frogs to shallow, marginal habitat types means that eventually the species will be wiped out by a drought (see Corn and Fogelman, 1984; and Fellers and Drost, 1993) that it would readily have weathered in refugia now pre-empted by alien species. Our hypothesis clearly predicts that this species will go extinct in southern Arizona, and probably elsewhere, unless appropriate action is taken.

Substantial records are available from SBNWR, Cochise County. This area is part of the Río Yaqui headwaters, and comprises five major natural springs and a series of managed artesian wells. The aquatic habitat areas vary from small to large spring runs with simple to deep, complex pools, with several large ponds and one area dominated by wet meadow. Both Chiricahua and lowland leopard frogs have been collected at this site. The area was long occupied by an array of exotic fishes (Hendrickson et al., 1980; D. Lanning, unpublished data; personal observations), and bullfrogs were privately introduced in the late 1940's (W. Glenn, personal communication) and documented by museum voucher by 1954. Since 1979, introduced fishes, including largemouth bass (Micropterus salmoides) were removed from all refuge ponds, and indigenous Yaqui River cyprinid and poeciliid fishes were re-established.

Chiricahua leopard frogs were historically collected at this site during the 1950's and 1960's, and James P. Collins obtained vouchers at the small springs and wet meadows as late as 1980, at which time large series of bullfrogs were obtained from pond habitats. We have not seen Chiricahua leopard frogs at

the site, despite intensive work 1985-1995 (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995). They apparently disappeared completely from the site during the early 1980's, shortly after establishment of the refuge. We did document lowland leopard frogs in 1985-1987 in central Black Draw, an open, shallow spring run, with few bullfrogs and primarily native fishes. The last leopard frogs we saw were juveniles dissected from bullfrog stomachs in 1988. In 1993 we learned that Chiricahua leopard frog populations had persisted in two stock ponds 5 and 11 km east of SBNWR, where introduced species were absent. Some of these frogs were re-introduced to the refuge, as described below.

The long lag time between introduction of exotic predatory species and the demise of the Chiricahua leopard frog population at SBNWR may be due primarily to interactions among the exotics. At Willow Pond, southeast of Portal, Cochise County, we observed a small population of adult bullfrogs and large numbers of newly metamorphosed young at a site with an abundance of largemouth bass, an expected situation because of the high fecundity of bullfrogs, the unpalatability of their tadpoles (Kruse and Francis, 1977; Kats et al., 1988; see Werner and McPeek, 1994), and the high palatability of metamorphosed bullfrogs. Moderate bullfrog populations are typically recorded in habitats with a diversity of predators (e.g., Clarkson and deVos, 1986; Currie and Bellis, 1969; Howard, 1978, 1981; personal observations in central Arizona). Such conditions probably occurred in parts of the refuge area prior to the removal of large predatory fishes. In contrast, remarkable densities of bullfrogs were found during our surveys: for example, we removed 204 adult bullfrogs totalling 51 kg from a 0.2 ha pond in two months during a dry season in 1994, with little or no terrestrial activity or immigration. At these population densities, bullfrogs of all stages and age classes occur in virtually every habitat type. We presume that release of the bullfrog population from most predation pressure led to the elimination of leopard frogs from local refugia that are now occupied by bullfrogs and bullfrog tadpoles.

To summarize, Chiricahua leopard frogs generally do not coexist successfully with bullfrogs or introduced predatory fishes. Table 2 indicates that Chiricahua leopard frogs have been significantly excluded or replaced by bullfrogs and centrarchid fishes. We have insufficient observations of mosquitofish or catfishes without bullfrogs and/or centrarchids to evaluate their impacts on Chiricahua leopard frogs at this time (Table 2), although we suspect that catfishes will almost always exclude Chiricahua leopard frogs. Our data indicate that the tiger salamander-leopard frog interaction requires further study to determine if and how long-term co-existence is possible. In contrast, leopard frogs coexist extensively with indigenous fishes (Table 1: Gila purpurea, Gila ditaenia, Poeciliopsis occidentalis, Agosia chrysogaster), with Sonoran mud turtles (Kinosternon sonoriense), and with native garter snakes (Thamnophis cyrtopsis, T. marcianus, and with T. eques prior to its disappearance from most lowland waters.

Bedrock Habitat and Water Quality. The Chiricahua leopard frog was rare or absent from perennial waters at carved bedrock ("plunge pool") habitats in the Santa Rita (rare in one, absent in two), Pajarito (rare in one), Chiricahua (absent in one), and Peloncillo (absent in one) mountains in 1994, despite an absence of introduced species. It was in this habitat, in the Santa Rita and Pajarito Mountains, that die-offs preceding extirpation of the Tarahumara frog (Rana tarahumarae) occurred during the 1970's and early 1980's; leopard frogs simultaneously declined or disappeared (Hale et al., 1995). Hale et al. (1995) measured high levels of arsenic and cadmium in water and sediments, and high levels of cadmium in frog tissue, and presented other evidence to support an acid rain hypothesis for cadmium toxicity.

We re-sampled water from these and other sites in 1994-5 (Table 3). Our results showed no elevated values for cadmium or arsenic. The heavy metal values for the 1990's (Table 3) are lower than

during the early 1980's (Hale et al., 1995, and therein), and we only detected arsenic once, copper three times, and zinc five times. The water we measured would not be expected to have toxic effects on frogs. However, relatively strong populations of leopard frogs in 1993-4 were found in water with high pH, hardness, and or total alkalinity, waters that would be expected to resist acidification and the concomitant cadmium toxicity that appears to have led to earlier ranid frog declines. The data in Table 3 are consistent with the hypothesis of Hale et al. (1995), and suggest that in the early 1990's, failure of successful recolonization by leopard frogs may be responsible for their current absence from bedrock plunge pool habitat areas that may be marginal for Chiricahua leopard frogs (personal observations) to begin with.

In early summer 1990, approximately 10-20 dead leopard frogs were observed at Sycamore Canyon, Pajarito Mountains (J. Carpenter, personal communication), suggesting a possibility of continuing episodic toxicity events. In general, however, bedrock plunge pool habitat may lack adequate shelter to support thriving populations of Chiricahua leopard frogs, and under the generally dry conditions prevailing since the mid-late 1980's in the study region, significance of failure to re-establish populations in this habitat type is unclear.

Re-introduction Efforts. In late spring 1993, a stock pond 11 km east of SBNWR containing Chiricahua leopard frog tadpoles appeared to be about to go dry. A total of 789 large tadpoles were transferred to seven perennial water sites on the refuge, all containing bullfrogs. The remaining tadpoles in the tank survived and reproduced successfully in 1993; however, no leopard frogs were observed on the refuge despite intensive sampling during 1993, 1994, and 1995, except in the enclosure described below.

In early spring 1994, just prior to drying of the same pond discussed above, refuge personnel and the private ranch owner salvaged 188 large tadpoles, one-half of the remaining few following a dry winter. The remaining half were artificially supplied with water on site (Cobble et al., 1995; The Nature Conservancy, 1995). Those salvaged were placed in a 0.75 ha bullfrog exclosure at SBNWR. The exclosure had four small ponds providing habitat similar to that elsewhere on the refuge, and were supplied with water from the pressurized aquifer sustaining most other wetlands on the refuge. We additionally installed netting that partially excluded herons from the ponds. Further details regarding construction of the new ponds and translocation results of the leopard frogs will be presented in a separate paper. An unknown number of leopard frogs escaped, and approximately 33 juvenile bullfrogs entered (all were subsequently removed), by climbing the exclosure fence prior to installation of eaves. At least 7 of the Chiricahua leopard frog tadpoles transformed and matured to participate in a successful breeding chorus in the enclosure on September 6, 1994. Twenty-seven progeny from this breeding plus two 2 yr-olds were counted in a breeding chorus on September 1, 1995.

The results of this re-introduction indicate that water quality was not responsible for the unsuitability of SBNWR habitat for Chiricahua leopard frogs during 1993-5. Although conditions were neither fully controlled nor replicated, there were two introductions into the refuge (the intentional one in 1993 and the presumed escapees from the enclosure in 1994), neither of which produced any observable survivors or breeding. Further, we observed successful survival or breeding at each of three nearby Chiricahua leopard frog populations during 1993-5, also in the absence of introduced species, although all three populations continued to decline under the influence of continued drought and low water levels.

II. Plains Leopard Frog.

Plains leopard frogs were found in three wetland complexes in Sulphur Springs Valley in 1993-4. In a large impoundment of Whitewater Draw, an abundant population co-existed with a modest bullfrog population and yellow bullheads (Ameiurus natalis) in Kovacs Lakes, a habitat with large seasonal fluctuations in areal extent. These frogs bred successfully during July 1993 and in spring or summer 1994, and at least several hundred juveniles were found in September 1994. During the drought of 1994, many of the catfish died (E. Kovacs, personal communication); and by September 1994 the bullfrog population had declined. We infer that these leopard frogs may be better able than bullfrogs and fishes to cope with the dramatic water level fluctuations, which probably approximate original conditions in the Sulphur Springs Valley prior to lowering of the water table by agricultural pumping.

In a mixed orchard-row crop area southwest of Willcox Playa, plains leopard frogs have persisted since at least 1974-5 (Frost and Bagnara, 1977; Clarkson and Rorabaugh, 1989), although Chiricahua leopard frogs have disappeared from the site. They are in two parallel linear ponds that are agricultural sumps separated by 0.5 km of plowed field. These ponds often go dry or fill rapidly, and the leopard frogs reappear quickly upon filling (D. Parizek, personal communication). Tiger salamanders were reported at this site in 1986-7 (Clarkson and Rorabaugh, 1989) but were not observed during the mid-1990's. The persistence of the frogs in these highly fluctuating waters may be characteristic for this species.

The plains leopard frog was also found in the wetlands created by the Arizona Electric Power Company ash-settling ponds in 1994, where both mosquitofish (Gambusia affinis) and tiger salamanders were also abundant. Plains leopard frogs were first reported at this site in 1986-7 by Clarkson and Rorabaugh (1989), who also reported possible bullfrog occurrence; Arizona Game and Fish Department ranid frog surveys failed to locate frogs in 1991-2; we did discover them in local areas with some difficulty in 1994. Co-existence of the leopard frogs and non-native species at this site may reflect the relative inefficiency of these predators(see Grubb, 1972; but also Kruse and Francis, 1977; Hammerson, 1982; and Sexton and Phillips, 1986). Moreover, power-plant activities probably result in periodic population collapses in various sections of the wetland, separated by levees; this and the high heterogeneity of habitat depth and vegetation structure also may allow the plains leopard frog in southeastern Arizona, unlike the Chiricahua leopard frog, to escape its enemies in time and space.

III. Lowland Leopard Frog.

The lowland leopard frog occurs on the periphery of the study region, and was observed at only two sites, at the base of the Rincon Mountains during our surveys in 1992-1994: there were no non-native species at either site. Historical localities for this species in Avra Valley, all farm ponds or stock ponds, now support bullfrogs, bullhead catfish, and mosquitofish. We are currently investigating the persistence of this species in abundance in natural desert streams where introduced bullfrogs, green sunfish, and yellow bullheads remain rare or fail to establish persistent populations.

CONCLUSIONS

We believe the data presented strongly indicate that a major and ongoing decline of the Chiricahua leopard frog in southern Arizona is the result of species introductions, primarily of bullfrogs and centrarchid fishes. We suspect that catfishes, and possibly trout, would be similarly detrimental, although we have no data directly bearing on this; other non-native species might also be detrimental to this frog.

We have no indication to suggest stable co-existence between the Chiricahua leopard frog and any alien species, although at least limited co-existence with tiger salamanders seems likely. Among the introduced species that may cause amphibian declines, it is likely that bullfrogs and crayfish will be the most difficult to eliminate from ecosystems, whereas fishes may be eliminated by drying or poisoning of habitats.

In every case where introduced species were recorded at a site, at least one of them was very abundant, excepting the two tiger salamander cases detailed above. A conspicuous factor in the strong negative effect of non-native on native species is the tremendous abundance achieved by non-natives in the absence of most major predators present in their natural ranges in eastern North America.

We have attempted to remove non-native bullfrogs from the SBNWR site, with marginal success thus far despite intensive efforts (Rosen and Schwalbe, 1995). Furthermore, non-native fishes on public lands are generally utilized for recreational fishing, currently precluding the radical, and difficult, removal efforts our data indicate are needed to recover Chiricahua leopard frog populations in many major wetland areas. This frog may thrive in perennial to semi-perennial stock ponds, which are usually isolated, artificial pools that can often be supplied with well water or dried as needed. Therefore, it may be possible and cost-effective to see the Chiricahua leopard frog through the current crisis by cooperating with ranching operation landholders to manage the waters they have created and/or maintain. Other threatened or endangered species, especially pond-breeding native fishes, could be integrated into such a program.

The use of stock ponds to assist in solving the crises of the aquatic fauna of the American West, while promising, is not a panacea. Scientists, land managers, and the public at large must be made aware of the seriousness of the introduced species problem. That would at least permit the removal of non-indigenous species from some manageable ranching landscapes, obviating continual removal of re-colonizing and re-introduced exotics. As a long term solution, preserving stream- and ciénega-pool species in artificial stock ponds seems unlikely to sustain the adaptive structure of the species. Recovery of indigenous species in natural habitat should be the primary goal for most or all endangered species, and the only apparent option for many.

We will need to understand how habitat modification and introduced species interact to damage native species populations (e.g., Jennings and Hayes, 1994; Minckley and Meffe, 1987). An understanding of key and unique species characteristics and dynamics in varied habitats, for example in the varying environmental responses of Chiricahua and plains leopard frogs described above, may be essential for successful restoration and management of species and their habitats. Understanding species natural history and physiology is critical to understanding their success or failure in the human-modified biosphere.

The arguments presented in this paper are not intended to discourage research into any other potential causes of amphibian decline, nor to suggest that other factors are not real and important. In fact, an interaction of factors could be more than additively harmful compared to single factor effects. Any cause that localizes a species makes it much more likely to be actually extirpated when challenged by another environmental problem, whether natural or human-caused.

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Table 1. Co-occurrence of the Chiricahua leopard frog with other aquatic vertebrates in southeastern Arizona, 1993-1994. Above the diagonal are the number of localities where co-occurrence was observed; below the diagonal are the proportional co-occurrences; the diagonal shows total number of occurrences for each taxon. A total of 107 sites is represented. Non-native species indicated by #.

	Rana catesbeiana	*R. chiricahuensis*	*R. blairi*	*R. yavapaiensis*	*Kinosternon sonoriense*	*K. flavescens*	*Thamnophis cyrtopsis*	*T. marcianus*	*T. eques*	*Scaphiopus sp.*	*Bufo punctatus*	*B. alvarius*	*Gastrophryne olivacea*	*Hyla arenicolor*	*Ambystoma tigrinum*	*Micropterus slamoides*	*Lepomis cyanellus*	*L. macrochirus*	*Gambusia affinis*	*Ameiurus melas*	*A. natalis*	*Ictalurus punctatus*	*Ctenopharyngodon idella*	*Gila ditaenia*	*Gila purpurea*	*Agosia chrysogaster*	*Poeciliopsis occidentalis*	*Rhinichthys osculus*	*Campostoma ornatum*	*Onchorhynkis mykiss*	*Salvelinus fontinalis*	*Pimephales promelas*
Rana catesbeiana#	**30**		1		8	2	4	3	1		1	1	3		1	7	4	5	8	2	2	1	1		3	2	1				
R. chiricahuenis		**19**			6		5	1			2	1	1	1	2		1							1	2	3	1	1				
R. blairi	.03		**4**			1		2							1				1		1										
R. yavapaiensis				**2**	1		2				1			1												1					
Kinosternon sonoriense	.27	.32		.50	**27**		8	2	1		4	3	4	4	1	3	7	4	5	1	1	1		1	2	5	1				
K. flavescens	07		.25			**10**		2		2					2		1		2												
Thamnophis cyrtopsis	.13	.26		1.0	.30		**16**	1		2	4	2	2	3		3	2	2	2		1		1		2	4	1				
T. marclanus	.10	.05	.50		.07	.20	.06	**7**	1	2		3				1	1		2	1	1				2	1	1				
T. eques	.03				.04			.14	**1**			1							1	1					1	1	1				
Scaphiopus sp.						.20	.13			**8**		1			1																
Bufo punctatus	.03	.11		.50	.15		.25				**7**	1	1	3				1						1	1						
B. alvarius	.03	.05			.11		.13	.43	1.0	.13	.14	**4**				1		1									1				
Gastrophryne olivacea	.10	.05			.15		.13				.14		**5**	2				1						1							
Hyla arenicolor		.05		.50	.15		.19				.43		.40	**6**										1		1					
Ambystoma tigrinum	.03	.11	.25	.00	.04	.20				.13					**13**				1												
Micropterus salmoides#	.23				.11		.19	.14				.25				**10**	3	5	6		1	1									
Lepomis cyanellus#	.13	.05			.26	.10	.13	.14								.30	**10**	1	4	1		3				2			1		1
L. macrochirus#	.17				.15		.13				.14	.25	.20			.50	.10	**8**	3		1	1			1	1			1	1		
Gambusia affinis#	.27		.25		.19	.20	.13	.29	1.0						.08	.60	.40	.38	**14**	1	1	1			1	1	1				
Ameiurus melas#	.07				.04			.14	1.0								.10		.07	**5**					1	2	1		2	1		2
A. natalis#	.07		.25		.04		.06	.14								.10		.13	.07		**3**										1
Ictalurus punctatus#	.03				.04											.10	.30	.13	.07			**1**									
Ctenopharyngodon idella#	.03						.06																**1**		1	1					
Gila ditaenia		.05			.04						.14		.20	.17										**1**							
Gila purpurea	.10	.11			.07		.13	.29	1.0		.14							.13	.07	.20			1.0		**5**	3	2				
Agosia chrysogaster	.07	.16		.50	.19		.25	.14	1.0					.17			.20	.13	.07	.40			1.0		.60	**10**	2		2			1
Poeciliopsis occidentalis	.03	.05			.04		.06	.14	1.0			.25							.07	.20					.40	.20	**2**					
Rhinichthys osculus		.05																										**2**			1	
Campostoma ornatum																	.10	.13		.40						.20			**3**	2		1
Onchorhyncus mykiss#																		.13		.20									.67	**2**		1
Salvelinus fontinalis#																												.50			**2**	
Pimephales promelas#																	.10			.40	.33					.10			.33	.50		**3**

Table 2. Correlative data for taxon-specific effects of introduced vertebrate species on the Chiricahua leopard frog. Numbers in the table are frequencies of occurrence of non-native species at localities where Chiricahua leopard frog populations (1--PRESENT) were extant in 1994, (2--ABSENT) had vanished as of 1994, or (3--also ABSENT) occurred in similar habitat within 10 km in 1994. Two occurrence localities for Chiricahua leopard frogs, with 2-3 adults and no evidence of a reproducing population, are excluded from this table (see text). Further, localities meeting criteria (2) and (3), but with more than one taxon category (as defined in the table) occurrence are also not included in this table.

	Chiricahua leopard frog population:		
Taxon	Present	Absent	Binomial probability
bullfrog	0 of 17	9 of 25	0.01
centrarchid fish	0 of 17	5 of 25	0.04
tiger salamander	1 of 17	5 of 25	0.21
salmonid fish	0 of 17	3 of 25	0.13
ictalurid, poeciliid, cyprinid fish	No comparisons available		----

Table 3. Water chemistry parameters for selected sites with leopard frogs, and nearby sites with perennial water but neither leopard frogs nor introduced species. Analysis was performed by Turner Laboratories, Inc., 1844 West Grant Road, Suite #104, Tucson, Az, 85745, according to Environmental Protection Agency Standard Drinking Water Analysis methodology. Leopard frog species in the table are **yav** = *R. yavapaiensis*, **chir** = *R. chiricahuensis*. A question mark indicates that the species occurs nearby but is not known from the site, probably because it had not been previously sampled. Abundance categories are **0** = absent, **1** = rare, **2** = uncommon, **3** = moderately common, **4** = abundant, and are based on sampling during 1993-4. Concentrations are in parts per million (mg/l); nd = below detection limit.

	date	species	abundance	pH	alkalinity	hardness	As	Cd	Ca	Cu	Pb	Mg	Me	Zn
detection limit:					1	1	0.005	0.003	0.2	0.02	0.005	0.1	0.001	0.04
Rincon metapopulation:														
Cienega Creek, Marsh Station	3/15/95	yav	4	7.80	233	507	nd	nd	146.0	nd	nd	33.4	nd	nd
Agua Caliente Cyn, Tucson	3/15/95	yav	3	7.45	22	23	nd	nd	7.7	nd	nd	1.9	nd	nd
Santa Rita metapopulation:														
West Sawmaill Canyon	6/25/95	chir	3	7.65	274	295	0.005	nd		nd	nd		nd	nd
Cave Creek	6/14/95	chir	1	7.61	173	180	nd	nd		nd	nd		nd	0.08
Gardner Canyon	6/14/95	chir	0	7.15	112	117	nd	nd		nd	nd		nd	0.11
Big Casa Blanca Canyon	6/14/95	chir	0	7.35	65	nd	nd	nd		nd	nd		nd	nd
Pajarito metapopulation:														
Garcia Tank, Altar Valley	5/16/95	chir	3	10.30	121	407	nd	nd		nd	nd		nd	nd
Yank Tank, Bear Canyon	5/16/95	chir	3	8.60	32	205	nd	nd		0.03	nd		nd	0.04
Sycamore Canyon spring	5/16/95	chir	2	7.82	73	272	nd	nd		0.03	nd		nd	nd
1 km below Sycamore Cyn spı	5/16/95	chir	1	7.18	72	302	nd	nd		0.03	nd		nd	nd
Chiricahua metapopulation:														
East Turkey Creek	7/19/95	chir	1	8.90	45	548	nd	nd	163.0	nd	nd	34.1	nd	0.04
Horshoe Pothole Canyon	7/19/95	chir?	0	6.00	4	24	nd	nd	6.9	nd	nd	1.6	nd	0.07
Peloncillo metapopulation:														
central Guadalupe Canyon	7/12/95	chir	2	7.00	130	148	nd	nd	51.6	nd	nd	4.7	nd	nd
Guadalupe Cyn Ranch Pond	7/12/95	chir	1	9.60	180	54	nd	nd	17.7	nd	nd	2.4	nd	nd
Spring of Contention	7/12/95	chir?	0	7.61	171	36	nd	nd	12.9	nd	nd	1.0	nd	nd